High-resolution last deglaciation record from the Congo fan reveals significance of mangrove pollen and biomarkers as indicators of shelf transgression

Scourse, J; Marret, F; Versteegh, GJM; Jansen, JHF; Schefuss, E; van der Plicht, J; Versteegh, Gerard J.M.

Published in:
Quaternary Research

DOI:
10.1016/j.yqres.2005.03.002

Available online at www.sciencedirect.com

SCIENCE DIRECT

Quaternary Research 64 (2005) 57–69

QUATERNARY RESEARCH

www.elsevier.com/locate/yqres

High-resolution last deglaciation record from the Congo fan reveals significance of mangrove pollen and biomarkers as indicators of shelf transgression

James Scourse[a,*], Fabienne Marret[a], Gerard J.M. Versteegh[b,1], J.H. Fred Jansen[b], E. Schefuß[c,2], Johan van der Plicht[d]

[a]School of Ocean Sciences, University of Wales (Bangor), Menai Bridge, Anglesey LL59 5EY, UK
[b]Netherlands Institute of Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands
[c]Marine Geosciences, University of Bremen, P.O. Box 330440, 28334 Bremen, Germany
[d]Centre for Isotope Research, University of Groningen, Nijenborgh 4, NL-9747 AG Groningen, The Netherlands

Received 4 May 2004
Available online 6 June 2005

Abstract

High abundances of mangrove pollen have been associated with transgressive cycles on tropical margins, but the detailed relations between systems tracts and the taphonomy of the pollen are unclear. We report here the occurrence and high abundance of *Rhizophora* pollen, in association with taraxerol, a *Rhizophora*-sourced biomarker, from a high-resolution Congo fan core covering the last deglaciation. An age model based on ^{14}C dates enables the temporal changes in taraxerol content and the percentage frequencies and flux (pollen grains (pg) cm^{-2} $(10^3\ yr)^{-1}$) of mangrove pollen to be compared quantitatively with the lateral rate of transgression across the flooding surface (derived from glacio-hydro-isostatic model output and the bathymetry of the margin). *Rhizophora* pollen concentrations and taraxerol content of the sediment are very strongly positively correlated with the lateral rate of transgression and indicate, independently of any sequence stratigraphic context, that mangrove pollen spikes are associated with the transgressive systems tract rather than the highstand systems tract or maximum flooding surface. Lower-resolution longer-term records from this margin indicate an association between taraxerol concentrations and transgressive rather than regressive phases. The flux of these materials to the Congo fan is interpreted as a function of the erosion of flooded mangrove swamp on the shelf and, less importantly, changing extent of mangrove habitat, during sea-level rise. Congo River palaeoflood events also result in reworking of mangrove pollen and supply to the fan, but this mechanism is subdominant. *Rhizophora* pollen has been underestimated in many palynological studies undertaken on cores from the African margin because of inappropriate sieve mesh size used during laboratory preparation.

Keywords: *Rhizophora*; Mangrove; Taraxerol; Sea-level; Transgressive systems tract; Tropical; Palynology

Introduction

Palynological investigations of cores and borehole cuttings from marginal marine, fan and shelf sequences in tropical and sub-tropical regions are often characterised by high quantities of mangrove pollen (Dupont and Agwu, 1991; Dupont et al., 2000; Grindrod et al., 2002; Lézine, 1997; Morley, 1995). The mangrove ecosystem characterises the inter-tidal environments of low energy coastlines in the tropics and subtropics and consists of a

* Corresponding author. Fax: +44 1248 716367.
E-mail addresses: j.scourse@bangor.ac.uk (J. Scourse), f.marret@bangor.ac.uk (F. Marret), gerardv@nioz.nl (G.J.M. Versteegh), jansen@nioz.nl (J.H.F. Jansen), schefuss@uni-bremen.de (E. Schefuß), plicht@phys.rug.nl (J. Plicht).
[1] Current address: Hanse-Wissenschaftskolleg, Lehmkuhlenbusch 4, D-27753 Delmenhorst, Germany.
[2] Current address: Department of Marine Chemistry and Geochemistry, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA.

0033-5894/$ - see front matter © 2005 University of Washington. All rights reserved.
doi:10.1016/j.yqres.2005.03.002

number of woody plant genera (e.g., *Rhizophora* and *Avicennia*) tolerant of salt and other physico-chemical stresses whose pneumorhizae systems are emergent during the lower part of the tidal cycle (Richards, 1996). Pollen produced by mangrove species is found, often in abundance, in shallow sub-tidal and inter-tidal sediments. Because mangrove often forms dense fringing vegetation within estuarine systems, mangrove pollen is also found in deeper marine sequences, such as fans, which are fed ultimately by fluvial distributaries and in which the mangrove pollen is supplied to the marine environment by fluvial transport (Dupont and Agwu, 1991; Dupont and Wyputta, 2003; Lézine, 1997). This flux of mangrove-derived organic material to marine sediments is also complemented by the relative abundance of taraxerol, which is strongly associated with *Rhizophora*, in such sediments (Versteegh et al., 2004). The past occurrence and abundance of mangrove can therefore be interpreted from combined palynological and organic geochemical analyses of ocean margin sequences.

The species assemblage of the west African mangrove ecosystem is of relatively low diversity (six genera and eight species) and high abundance but is nevertheless regionally variable. In central west equatorial Africa, the mangrove typically consists of the genera *Avicennia* and *Rhizophora* with subdominant *Laguncularia* and *Conocarpus*. The subdominant species are not significant contributors to the pollen record and even *Avicennia* produces pollen in low quantities and has low representation in marine sediments (Dupont and Weinelt, 1996; van Campo and Bengo, 2004). *Rhizophora* pollen (Fig. 1), on the other hand, is produced in very large quantities

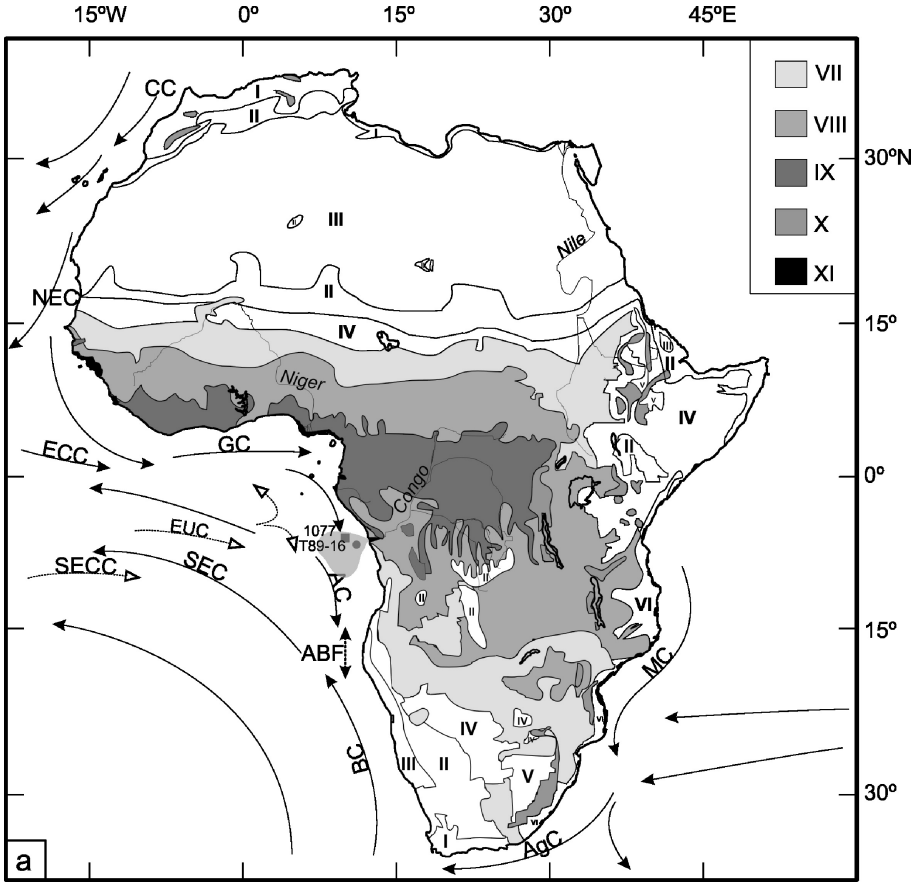

Figure 1. (a) Location map of cores T89-16 (filled circle) and ODP 1077 (filled square) with oceanographic and vegetational context. Surface oceanic currents and fronts: Canaries Current (CC), North Equatorial Current (NEC), South Equatorial Counter Current (SECC), South Equatorial Current (SEC), Benguela Current (BC), Angola Current (AC), Equatorial Counter Current (EUC), Guinea Current (GC), Angola-Benguela Front (ABF), Mozambique Current (MC), Agulhas Current (AgC). The Congo plume is outlined in grey. Vegetation zones: Mediterranean (I); Transitional semi-deserts (II); Deserts (III); Transitional deserts-grasslands (IV); Temperate and mountain grassland (V); East Africa coastal forest (VI); Sudanian woodland and dry forest and Zambezian dry forest and woodland (VII); Guinea-Congolia/Sudania transitional forest and Guinea-Congolia/Zambezia transitional forest (VIII); Guineo-Congolian lowland rainforest and swamp forest (IX); Afromontane vegetation (X) modified after White (1983). Mangrove is outlined in black along the coast. (b) Bathymetry (m) for the Congo shelf and slope to the north of the Congo canyon (10 m isobaths) showing location for which sea-level data have been extracted from Peltier (1994) and region within which data have been digitised to calculate the rate of lateral transgression. Location of core T89-16 at a water depth of 824 m is to the west of the digitised map.

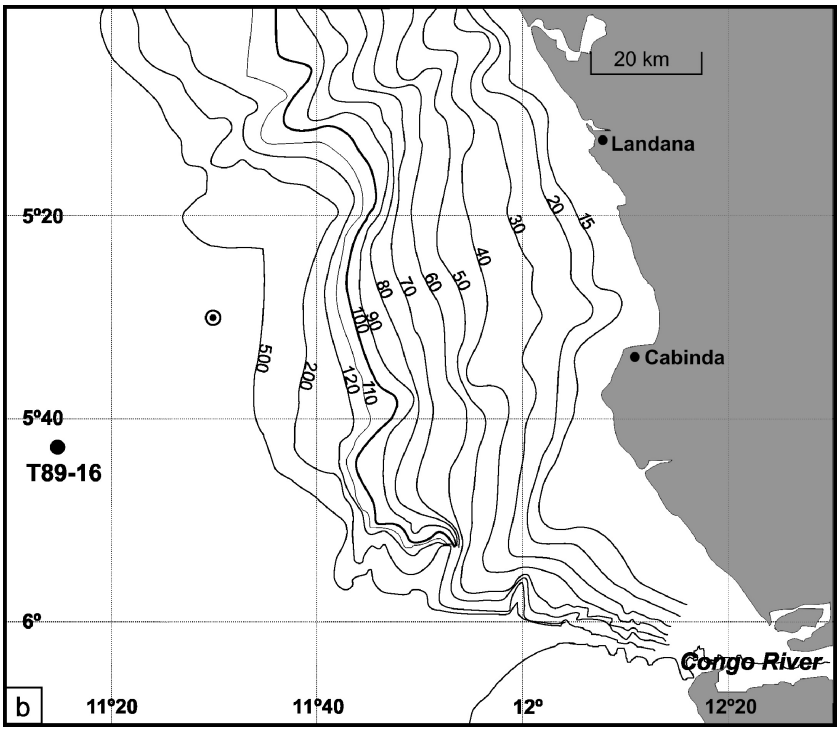

Figure 1 (*continued*).

and is often preserved in abundance in sediments. The past occurrence of the mangrove system along this margin is therefore based largely on the abundance of *Rhizophora* pollen (Dupont and Agwu, 1991; Dupont et al., 2000) supplemented by the novel biomarker method which is itself linked to *Rhizophora* (Koch et al., 2005; Versteegh et al., 2004).

A number of studies have highlighted the association between increased *Rhizophora* abundances and deglaciation (Dupont et al., 2000; Jahns, 1996; Lézine and Vergnaud-Grazzini, 1993; Marret et al., 2001; Shi and Dupont, 1997; van Campo, 1986; van der Kaars et al., 2000) whilst some (e.g., Ellison, 1989; Grindrod et al., 1999, 2002; Lézine, 1997) have used the abundance of mangrove pollen within peats and shallow marine sequences as an indicator of relative sea-level change. Palynological investigation of tropical and subtropical hydrocarbon exploration wells, in conjunction with associated sub-bottom seismic data, has revealed associations between mangrove pollen and systems tracts (Germeraad et al., 1968; Morley and Richards, 1993). Interest in mangrove from such studies is accentuated by the suggestion that mangrove-litter is known to be very waxy and lipid-rich and is thought in regions such as the Niger Delta to constitute a significant oil source (P.A. Ventris, personal communication, 2004). Whilst some studies identify a general association between high mangrove pollen and the maximum flooding surface associated with the humid (interglacial) component of Quaternary climate cycles (e.g., Fredoux, 1994; Pickett et al., 1997; Poumot, 1989; van der Zwan and Brugman, 1999), others associate mangrove spikes specifically with transgressive systems tracts (e.g., Armentrout et al., 1999; Hoorn, 1994). Ventris (in Armentrout et al., 1999) goes further and identifies high abundance occurrences during the late lowstand-early transgressive phase of slow relative sea-level rise and also during the highstand phase of relative sea-level. The former occurs when much of the coastal plain is aggrading and supporting a wide mangrove belt, and the latter is associated with progradation. Conversely, in Ventris' view, the maximum flooding surface condensed section is associated with low mangrove abundances, interpreted to be a result of maximum inundation of the coastal plain and constriction of the mangrove belt. Armentrout et al. (1999) find no association between the mangrove assemblage and their interpretation of the late lowstand and early transgressive intervals. There is therefore general agreement that mangrove is associated with transgression, but disagreement as to the association between high mangrove abundances and the precise stage of transgression.

Spikes of mangrove pollen have, in some cases, been used as indicators, or confirmation, of transgressive systems tracts (e.g., Armentrout et al., 1999; Morley, 1995; Poumot, 1989; van der Zwan and Brugman, 1999). The inference is that transgression across the shelf results in the creation of habitat suitable for mangrove colonisation, and therefore supply of mangrove pollen. In studies

which lack a sequence-stratigraphical context, however, there is often little independent evidence to corroborate the inference that such mangrove spikes are linked to transgression and there is therefore a danger of a circularity of argument. This is notably the case with palaeoenvironmental studies of the African equatorial Atlantic margin. Furthermore, in addition to habitat extension, it is probable that the primary supply of mangrove pollen is complemented by erosion of pre-existing mangrove-rich coastal/estuarine sediments inundated on the submergent shelf and by the penecontemporaneous reworking of newly deposited mangrove pollen in inter- and sub-tidal environments (Versteegh et al., 2004). Also, existing analyses of the relations between the rate of sea-level rise and mangrove/taraxerol abundance (e.g., Versteegh et al., 2004) refer only to the absolute amount of eustatic rise per unit time. This ignores the critical parameter which is the lateral rate of transgression across the flooding surface, a function of relative sea-level rise and the hypsimetric curve for the respective continental margin.

The lack of high-resolution temporal control, of independent evidence on the rate and timing of sea-level change, and of detailed bathymetric data in previous studies has precluded analysis of this problem. We report here data on the occurrence and high abundance of *Rhizophora* pollen, in association with taraxerol, from a high-resolution Congo fan core covering the last deglaciation. An age model based on ^{14}C dates enables the temporal changes in the percentage frequencies and flux (pollen grains (pg) cm^{-2} $(10^3\ yr)^{-1}$) of mangrove pollen, and in biomarkers, to be compared with pre-existing independent data on relative sea-level change in this region and with the hypsimetric curve for the Congo margin. This approach therefore provides a basis with which to test the hypothesis that high quantities of mangrove pollen can be used as an indicator of transgression across tropical and sub-tropical continental shelves, enables the precise relations between mangrove abundances and the stage of transgression to be identified, and also provides data to test the competing hypotheses of habitat extension and sediment reworking.

Materials and methods

Piston core T89-16 (5°42.2′S–11°14.1′E) was recovered from 824 m water depth, north of the Congo river mouth (100 km offshore) at the fringe of the Congo river plume (Fig. 1a) and consists throughout of hemipelagic mud. Previous papers on this core report summary pollen and dinoflagellate cyst stratigraphy (Marret et al., 1999) and the interpretation of Congo palaeodischarge fluctuations from the proxy data (Marret et al., 2001). The age model adopted is based on 17 AMS ^{14}C dates on the bulk carbonate fraction (Fig. 2); further details are provided in Marret et al. (2001).

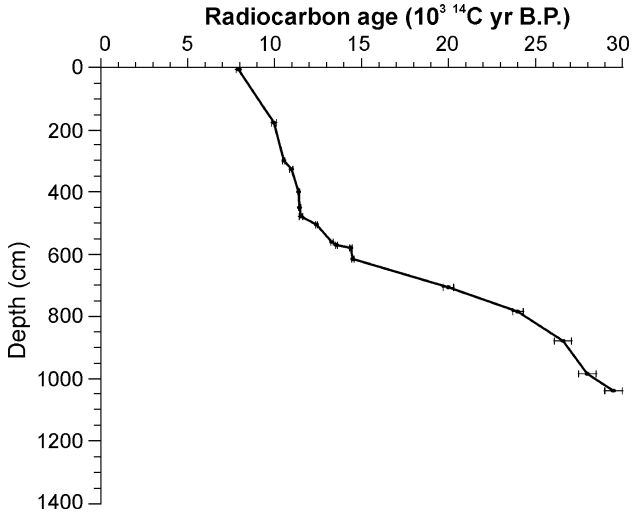

Figure 2. Age-depth curve for Congo fan core T89-16. The marine reservoir correction (402 yr) is based on the CALIB4.3 (Stuiver et al., 1998) recommendation for this region; this is supported by a 400-yr offset in oxygen isotopic spikes between this core and uncorrected dates on bulk organic (largely terrestrial) (Barusseau et al., 1988) matter on overlapping sections of nearby core GeoB 1007-4 (see Marret et al., 2001) for the period 12,000 to 9000 ^{14}C yr B.P.

Samples were initially prepared for palynological analyses following standard procedures (chemical treatment with cold HCl and HF but without acetolysis; sieving at 10 μm). However, comparative preparations clearly demonstrated loss of *Rhizophora* and other small pollen grains (10–20 μm size) with a standard 10-μm mesh sieve. A 5-μm mesh sieve was therefore adopted for pollen analyses with a consequent increase in the representation of *Rhizophora* (see Appendix A). The implication of this finding is that published palynological records from this margin which used a 10-μm mesh sieve during preparation may have seriously underestimated the frequencies, concentrations and fluxes of mangrove pollen. Previous studies have alluded to this problem (e.g., van der Zwan and Brugman, 1999) but recommend adoption of a 10-μm sieve over the even larger 15-μm sieve. A minimum of 100 pollen grains was counted, but for most levels totals in excess of 300 were attained.

The abundance of taraxerol relative to other land-derived lipids in surface samples and sediment cores from the Cape and Angola basins (southeast Atlantic) covaries with the relative abundance of *Rhizophora* pollen (Versteegh et al., 2004). This covariance, together with the very high concentrations of taraxerol in the leaves of *Rhizophora mangle* and *R. racemosa*, indicates that taraxerol can be used as a proxy for *Rhizophora* in addition to the pollen itself. We have analysed the taraxerol abundance in this core and present the data as ratios with two general lipids representative of higher plant leaf waxes, C_{28} alcohol and C_{29} alkane, in order to compensate for the input of taraxerol from plants other than *Rhizophora*. Alkane is the more resistant compound and may have a higher proportion of

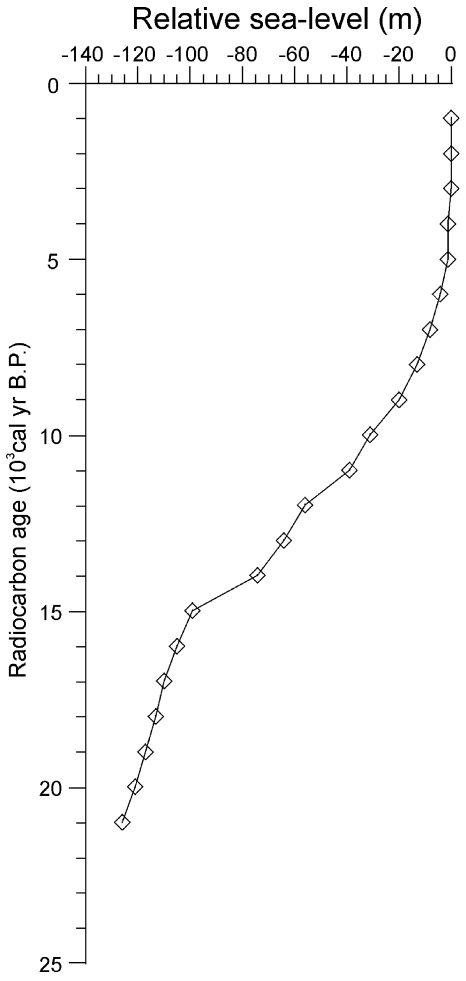

Figure 3. Relative sea-level curve for location (5° 30′ S, 11° 30′ E) on the Congo margin extracted from Peltier (1994) in calibrated years B.P.

wind-transported rather than water-transported molecules. The methods used to analyse the biomarkers are presented in Versteegh et al. (2004).

We have compared the dated palynological record with published data on relative sea-level change for the Congo region over the last deglaciation. No long observational records of sea-level change for this region exist, so we have extracted the relevant relative sea-level data (Fig. 3) from a widely available global isostatic model database (Peltier, 1994; http://ingrid.ldgo.columbia.edu/sources/.peltier/) for a representative location (5°30′ S, 11°30′ E) on the Congo shelf proximal to the T89-16 core site (Fig. 1b). Though these model data are not constrained by sea-level index points for this margin, the model domain is global and multiple sea-level datasets from other regions have been used to constrain the model. Although the Congo region has not been subject to large isostatic movements since the Last Glacial Maximum (LGM), this sea-level reconstruction is more rigorous than simply using the Barbados relative sea-level curve (Fairbanks, 1989) because deglacial isostatic readjustments to ice and water loading and unloading are global in extent (Lambeck, 1986). The best available regional bathymetry for the Congo shelf and slope is from Giresse (1980) (Fig. 1b).

Results and discussion

Figure 4 shows the frequencies of *Rhizophora* pollen from 23,000 to 9000 cal yr B.P., spanning the last deglaciation. Apart from a large single-sample spike at 22,000 cal yr B.P., values are low, less than 20%, from 23,000 until 16,000 cal yr B.P. Soon after 16,000 cal yr B.P. values rise sharply to 40%, followed by a steady increase that continues until the highest values in excess of 80% are reached after 12,500 cal yr B.P. Values then remain high until a decline which starts at 10,500 cal yr B.P. By 9000 cal yr B.P. values have fallen back to 60%. Though values remain high between 12,500 and 10,500 cal yr B.P., the record is quite variable and spikes of ~10–15% characterise this maximal part of the record. The percentage frequencies of *Rhizophora* pollen are so high in these sediments that, for interpretation of the remaining components of the palynological record (Marret et al., 2001), a pollen sum excluding *Rhizophora* has been used.

The taraxerol record (Fig. 4b) is very strongly positively correlated with the *Rhizophora* pollen record (Versteegh et

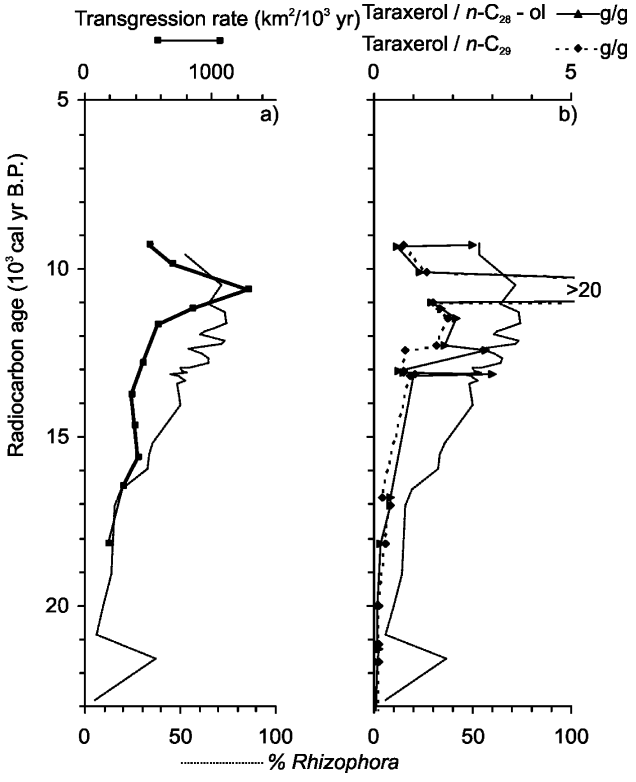

Figure 4. *Rhizophora* percentage frequencies (based on pollen sum for all plants excluding spores), ratios of taraxerol to C_{28} alcohol and C_{29} alkane, and rate of lateral transgression curve (km^2 (10^3 yr)$^{-1}$) for the Congo shelf based on relative sea-level curve from isostatic modelling (Peltier, 1994). Ages in calibrated yr B.P.

al., 2004). The ratios of both taraxerol to C_{28} alcohol and C_{29} alkane rise in concert with *Rhizophora* percentages from a low at the LGM to a single major peak at 11,000 cal yr B.P. coinciding with the latter part of the *Rhizophora* maximum. The decline from these peak values after 11,000 cal yr B.P. is also reflected in the taraxerol record.

Flux data for selected terrestrial proxies are presented in Figure 5. These show distinctive pulsed increases for all proxies centred on 16,500, 13,400 and 13,000 cal yr B.P. Marret et al. (2001) have compared these data with sedimentation rates and marine proxies (dinoflagellate cyst fluxes, planktonic foraminiferal $\delta^{18}O$ ratios, $U^{K'}_{37}$ sea-surface temperature and alkane/alkenone ratio) and interpreted these features as major palaeodischarge pulses of the Congo River, perhaps linked to precipitation change forced by latitudinal migration of the Inter-Tropical Convergence Zone (ITCZ). *Rhizophora* pollen does not form an important component of the 16,500 cal yr B.P. spike but it is the dominant component of the later, larger, spikes at 13,400 and 13,000 cal yr B.P.

There are two possible mechanisms to explain the record of *Rhizophora* in this core: (1) that the mangrove pollen has been supplied to the fan predominantly by fluvial distributaries from the estuary and therefore reflects Congo river palaeodischarge, (2) that the mangrove pollen has been supplied directly to the marine environment all along the coastal fringe and that the record reflects relative sea-level rise. In this latter situation, it is envisaged that during eustatic lowstands mangrove would have been restricted to a very narrow fringe along the outer continental shelf and along the rather deeply incised Congo channel across the shelf (Giresse et al., 1982) and that as sea-level rose the habitat for mangrove expanded as the shelf was flooded. Ultimately, at highstand, the habitat was once again restricted because the upper slope of the shelf is again rather greater than over the majority of the shelf (Fig. 2). In this way, the mangrove habitat extent is controlled by the lateral rate of transgression which is a function of the morphology of the shelf (the local hypsimetric curve) and the rate of local relative sea-level rise. In addition to direct supply from mangrove to the marine system and penecontemporaneous reworking of mangrove pollen, it is to be expected that older mangrove sediments submerged by sea-level rise would be reworked

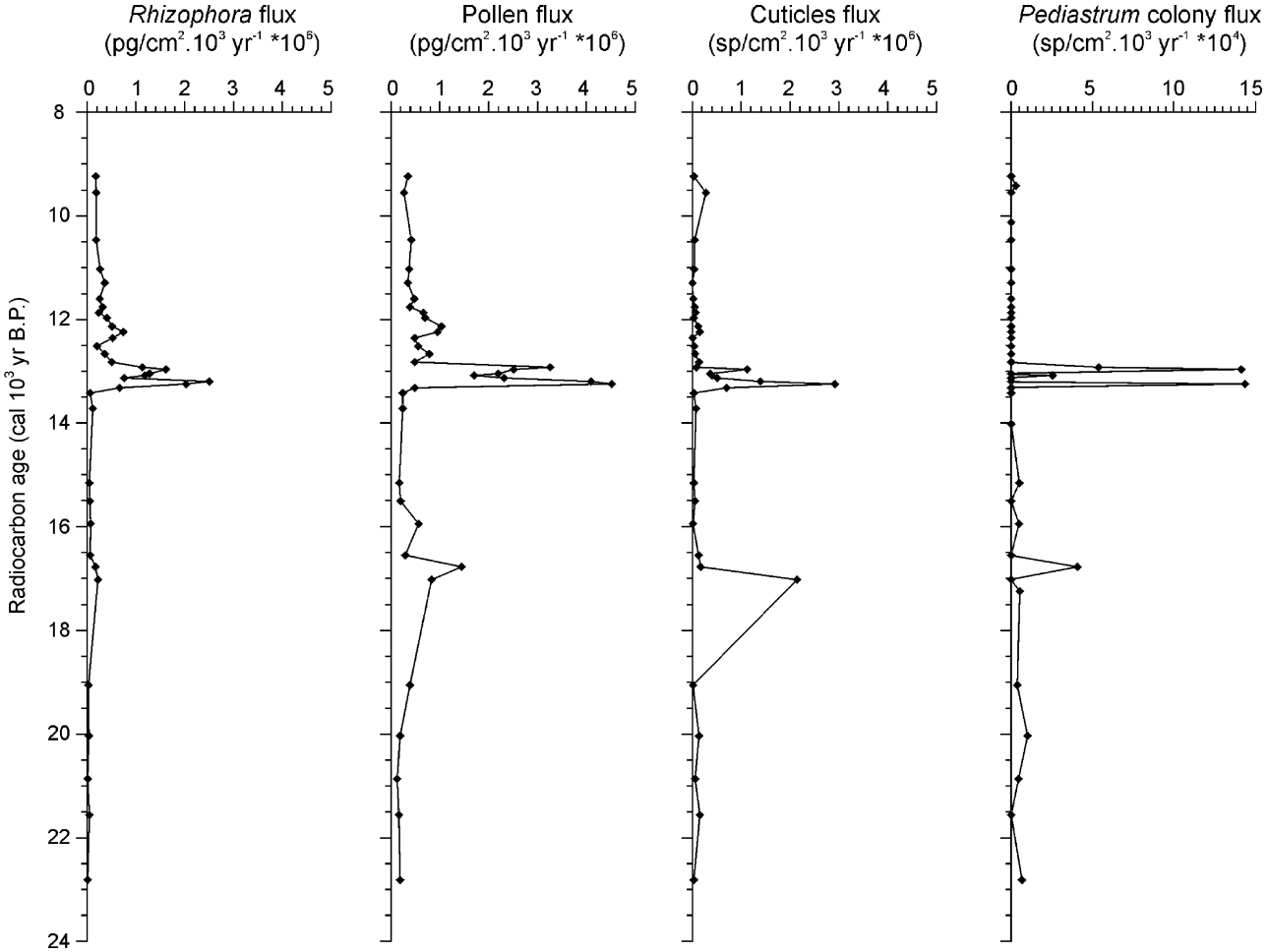

Figure 5. *Rhizophora*, total pollen, cuticle and *Pediastrum* fluxes for the period 23,000 to 9000 cal yr B.P. For the period 18,000 to 9000 cal yr B.P. sample resolution is 100–200 yr.

in the inter-tidal and sub-tidal zones and further contribute reworked mangrove pollen to the ambient marine sediments, including the fan.

In order to analyse the record with respect to these competing sources, we have compared the *Rhizophora* record against the rate of lateral transgression across the flooding surface calculated from the regional bathymetry (Fig. 1b) and the relative sea-level curve (Peltier, 1994). For this calculation, we have defined a representative area of coast, shelf, shelf break and upper slope (Fig. 1b) and digitised this area in order to calculate the area in km^2 defined by the isobaths (Table 1). Using the relative sea-level curve (Fig. 3), we have then calculated the rate of lateral transgression, in km^2 $(10^3$ yr$)^{-1}$, across the Congo shelf between 18,000 and 9000 cal yr B.P. (Fig. 4a).

The lateral transgression data demonstrate that as sea-level started to rise after the LGM, between 18,000 and 16,000 cal yr B.P. initially the rate was rather low, between 200 and 400 km^2 $(10^3$ yr$)^{-1}$, not because global eustatic sea-level was not rising fast (cf. Fairbanks, 1989), but because the slope of the outer shelf and upper slope in this region, as in many other places, (Fig. 2) is rather steep. Between 16,000 and 14,000 cal yr B.P. the rate of transgression declined to less than 400 km^2 $(10^3$ yr$)^{-1}$ after which there was an increase to nearly 600 km^2 $(10^3$ yr$)^{-1}$ at just after 12,000 cal yr B.P. The fastest rates of lateral transgression, when the rising sea-level was flooding the shallow gradient of the shelf most rapidly, were recorded between 12,000 and 10,500 cal yr B.P., reaching a peak rate of almost 1300 km^2 $(10^3$ yr$)^{-1}$ at 10,500 cal yr B.P. The rates dropped back to 500 km^2 $(10^3$ yr$)^{-1}$ by 9000 cal yr B.P.

The comparison with the *Rhizophora* percentage frequency curve and the taraxerol record is striking (Fig. 4b). Apart from the high-frequency fluctuations around 13,000 cal yr B.P., the fluctuations in *Rhizophora* percentages and taraxerol relative abundance reflect directly the changes in the rate of lateral transgression across the shelf. The decline in the rate of transgression after 16,000 cal yr B.P. correlates with a check in the increase in *Rhizophora* percentages at the same time, and the start of the decline in percentages at 10,500 cal yr B.P. is synchronous with the marked decline in the rate of transgression. The large peak in taraxerol at 11,000 cal yr B.P. coincides exactly with peak transgression rate. We conclude from this correlation that *Rhizophora* percentages and taraxerol abundance are strongly linked to the rate of lateral transgression across the shelf. We interpret this to be a function of both the rapid spread of mangrove habitat across the rapidly flooding but gently sloping shelf during transgression and to the erosion of flooded and newly submergent mangrove swamps. Mangrove habitat is restricted during early transgression by the relatively steep outer shelf and upper slope and similarly habitat is restricted by the coastal morphology once the highstand has been attained.

Table 1
Inter-isobath extent (km^2) based on digitised region (Fig. 1b) of Congo slope, shelf and coast

Isobaths (m)	Inter-isobath extent (km^2)
15 to 20	411.0
20 to 30	616.1
30 to 40	716.9
40 to 50	538.3
50 to 60	468.8
60 to 70	431.5
70 to 80	333.0
80 to 90	324.8
90 to 100	348.6
100 to 110	346.0
110 to 120	408.3

ODP Site 1077 (5°10.8′ S, 10°26.2′ E) (Fig. 1a) (Dupont et al., 2001; Jansen and Dupont, 2001) drilled ~275 km off the Congo River mouth at a water depth of 2384 m, provides a longer-term lower-resolution record of taraxerol (from Versteegh et al., 2004) against sea-level based on $\delta^{18}O$ on benthic foraminifera (from Shackleton et al., 1991) for the period between 0.46 and 1.25 myr ago (Fig. 6). These data clearly indicate the association between high taraxerol content and transgressive phases; regressive phases are inversely correlated with taraxerol. Similar resolution pollen analyses from this margin (e.g., Dupont et al., 2000) also indicate that *Rhizophora* spikes are associated only with transgressive and not with regressive phases. Both regression and transgression result in expansion of shelf habitat for mangrove development, but only transgression results in extensive shelf-wide erosion of mangrove ecosystems by inter-tidal and shallow sub-tidal, notably wave base and tidal, processes during flooding. Erosion of mangrove-rich sediments during regressive emergence and lowstand conditions is focussed only along channel distributaries, leaving the mass of mangrove muds preserved on the emergent shelf. The relationship with transgressive/regressive conditions strongly suggests that the *Rhizophora* signal reported here is dominated by erosion of penecontemporaneous material rather than extension of habitat and emphasises the association between *Rhizophora*/taraxerol spikes and transgression. Regressive mangrove swamps would, furthermore, be eroded during the succeeding transgression implying that some of the *Rhizophora* pollen and taraxerol may be even older and derive from the previous climate/sea-level cycle.

The speed of sea-level rise sets additional limits on the expansion of the mangrove ecosystem (Versteegh et al., 2004). With increasing rate of sea-level rise, the time available between germination and drowning decreases. Since it takes several years before a newly-established *Rhizophora* plant can reproduce, it is possible that under conditions of very rapid sea-level rise the flowering stage is not attained before submergence. In such circumstances, only plants established at the uppermost marine

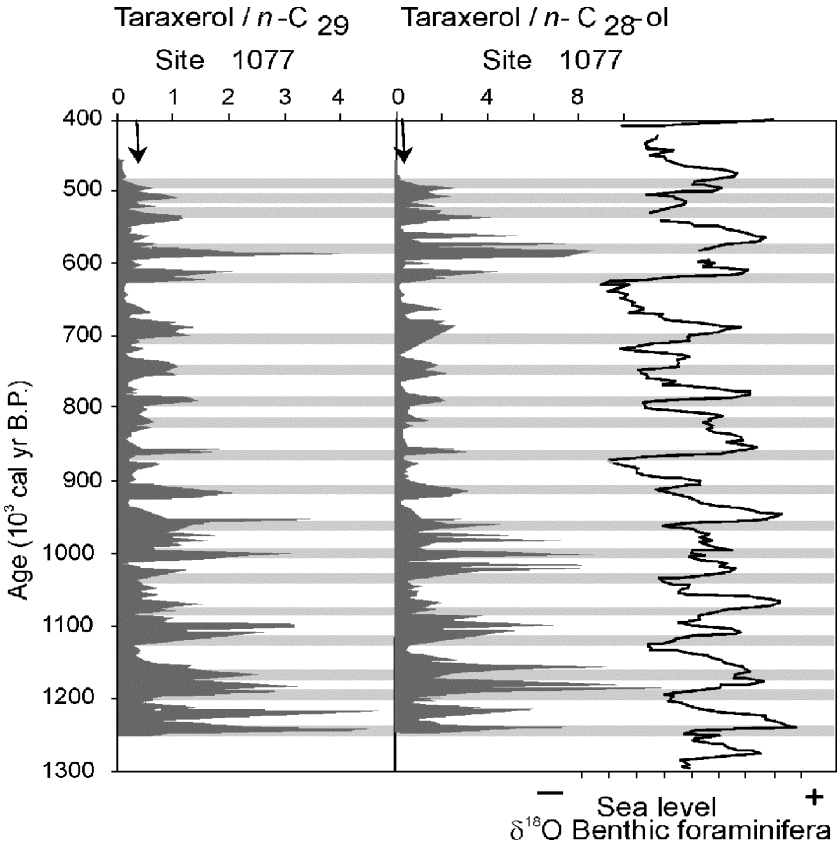

Figure 6. Taraxerol as g/g ratios against higher plant leaf wax lipids, n-C_{28} alcohol and n-C_{29} alkane, plotted with smoothed $\delta^{18}O$ benthic foraminiferal record (as proxy for sea level) (Shackleton et al., 1991) at ODP Site 1077. Transgressive phases highlighted. Note that high taraxerol is positively correlated with transgressive phases.

limit may survive long enough to reproduce prior to drowning. The number and also the age (size, number of flowers per tree) of adult trees will decrease with increasing rate of sea-level rise, and both will decrease pollen production. Therefore, in the absence of reworking, *Rhizophora* pollen does not reflect population size but rather the number of *Rhizophora* flowers (Versteegh et al., 2004). During periods of rapid sea-level rise, the influence of the area available for the mangrove ecosystem will therefore be overemphasised due to the increased stress on both tree survival and pollen production. This conclusion supports the notion that much of the *Rhizophora* signal in this record from the Congo derives from reworked sources.

It is clear, however, from the flux data (Fig. 5) that changes in Congo River palaeodischarge also partly control the supply of *Rhizophora* pollen to the fan. *Rhizophora* flux is not independent of the flux spikes in the other proxies which have been linked to palaeodischarge events (Marret et al., 2001). It is perhaps significant that *Rhizophora* does not contribute to the 16,000 cal yr B.P. event as much as it does to the later events at 13,400 and 13,000 cal yr B.P. If the above interpretation is correct, by 13,400 cal yr B.P. mangrove was well established in a broad zone across the shelf, and probably also in the estuary of the Congo. Furthermore, extensive areas of newly flooded mangrove swamp were by then in existence. Any large flood of the Congo would inevitably erode these sources with the resultant supply of *Rhizophora* pollen, and other terrestrial materials, to the fan. Conversely, at 16,000 cal yr B.P. mangrove habitat was more restricted in extent; newly flooded mangrove swamp was less extensive due to the slope morphology, causing it to be less subject to intertidal and shallow sub-tidal erosion than the flooded swamps later submerged at higher elevations closer to the present coast.

These results reflect the findings of Grindrod et al. (2002) in a parallel study of mangrove vegetation histories from shelf and deep ocean sequences adjacent to northern Australia. Coincident findings include the strong mangrove pollen signals in ocean cores coincident with periods of significant sea-level rise, minimal mangrove sequences on the steeper continental slope shorelines of the early transgressive phase, widespread mangrove associated with transgression across the low gradient continental shelf, and relatively restricted mangrove corresponding with sea level highstands. Less emphasis is given in Grindrod et al. (2002) to reworked mangrove material in the deep ocean sequences given the palynological evidence from intact mangrove sequences preserved on the continental shelf.

Conclusions

The supply of mangrove pollen, dominantly *Rhizophora*, and *Rhizophora*-derived taraxerol, to the Congo fan is dominantly a function of the erosion of flooded mangrove swamp on the shelf and, less importantly, changing extent of mangrove habitat, during sea-level rise.

The extent of mangrove habitat is a function of the rate of lateral transgression which is controlled by relative sea-level change and the regional morphology of the continental shelf.

Table 2
Counts of pollen grains found in the fractions between 5 and 10 μm and above 10 μm

Core T89-16	35 cm		98 cm		642 cm		707 cm	
Sieve	>5 <10	>10	>5 <10	>10	>5 <10	>10	>5 <10	>10
Acacia				2				
Alchornea	7		8		7	1	4	
Allophylus			2				1	
Altenanthera	1							
Araliaceae			1					
Asteraceae liguliflorae						1		
Asteraceae tubuliflorae	1				5	3	1	2
Canthium					1			
Caryophyllaceae		1			1			
Cassia		1		2		1		
Celtis			1		1		1	
Chenopodiaceae	1							
Cochlospermum type			1					
Combretaceae	7		1	1	8		3	
Cyperaceae	4	5	2	16	65	83	40	57
Diospyros						1		
Dobera			4	1	2		2	
Ebenaceae		1						
Euphorbiaceae		1				1		3
Fagara				1				
Ficus	1							
Hymenocardia	2							
Isoberlinia						1		
Poaceae		11	4	27	10	104	11	63
Lannea					1		1	
Liliaceae								1
Macaranga Type	2		1					
Manilkara				1	1			
Myrica							1	
Myrtaceae				1				
Nauclea	2		3		2		3	
Oleaceae		1				1		
Pseudarthia		1						
Podocarpus		40	1	46		87	3	76
Rhizophora	94	1	101	7	26		7	
Rubiaceae				1				
Rullia		1				2		
Salvadoraceae	3	1	1					
Sapindaceae		1		1			1	1
Schrebera				1				
Schefflera			1					
Securinega	1							
Syncepalum			1					
Syzygium	2		1		3		1	
Tamarindus						1		
Tetrochidium				1		1		
Uapaca				2			1	
Unidentified pollen grains	47	1	33	16	22	18	36	3
Monolete spores	15	37	5	54	63	209	34	114
Trilete spores	1	17		37	1	100	1	52
Pollen Sum	175	67	167	125	155	306	117	206
Spore Sum	15	74	5	91	64	309	35	163

Congo River palaeoflood events also result in reworking of mangrove pollen and supply to the fan, but this mechanism is subdominant.

Rhizophora and taraxerol spikes can be unequivocally linked to transgression. This study provides independent support for the notion that mangrove pollen spikes indicate transgressive systems tracts.

Rhizophora and taraxerol spikes are therefore linked to the rate of sea-level rise and inundation of mangrove swamps, and record maximal rates of lateral transgression rather than highstand conditions or the maximum flooding surface. Once highstand is attained, *Rhizophora* frequencies and fluxes are already in decline. During Late Pleistocene interglacial stages, *Rhizophora* and taraxerol maxima record early interglacial and not mid- or late-interglacial conditions.

Rhizophora pollen has been underestimated in many palynological studies undertaken on cores from the African margin because of inappropriate sieve mesh size used during laboratory preparation.

Acknowledgments

This work was supported by a UK Natural Environment Research Council Small Research Grant (GR9/02631) and a major grant from the Leverhulme Trust (F/00 174/E) both of which are gratefully acknowledged. We thank Katsuto Uehara (Research Institute for Applied Mechanics, Kyushu University, Fukuoka, Japan) for help with abstracting the sea-level curve for the Congo outflow region, and to Paul Ventris, Bob Morley and Lydie Dupont for useful discussion. Reviews by Lydie Dupont and John Grindrod significantly improved the manuscript. This is in part a contribution within the framework of the Netherlands-Bremen Oceanographic Cooperation (NEBROC).

Appendix A. *Rhizophora* pollen and sieve mesh size used in palynological preparation

Preparation: four samples were selected from depths 35, 98, 642 and 707 cm from core T89-16 (Table 2). The first two samples are located in the early Holocene part of the core, whilst the other two record the LGM. Wet and dry weights as well as volume of the four sediment samples were measured and tablets of exotic marker spores (*Lycopodium clavatum*) were added in order to estimate palynomorph concentrations. Samples were then successively chemically treated with cold HCl (10%) and cold HF (32%) in order to remove carbonate and silicate fractions. The residue was passed through superimposed monofilament mesh sieves of 10 and 5 μm aperture (Nycra type). Short digestion by KOH (less than 5 min) was performed prior to sieving to facilitate the sieving process. Residues of fractions between 5 and 10 μm, and >10 μm, were mounted in glycerine jelly stained with fuchsin.

Appendix B. Results

B.1. Fraction between 5 and 10 μm

In samples 35 cm and 98 cm, *Rhizophora* pollen grains were found in abundance (Figs. 7 and 8, Table 2), constituting more than 50% of the two spectra. *Rhizo-*

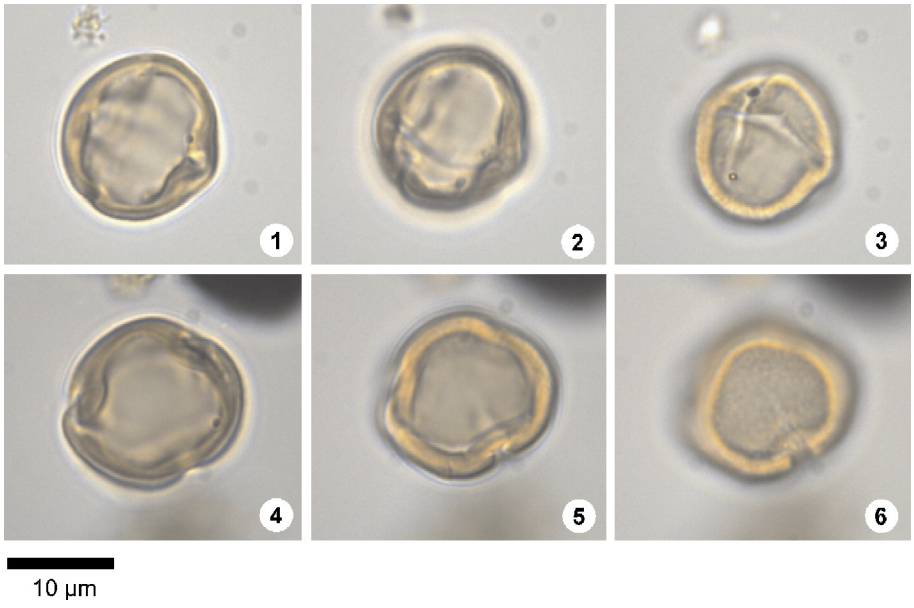

Figure 7. Light microscope images of *Rhizophora* pollen.

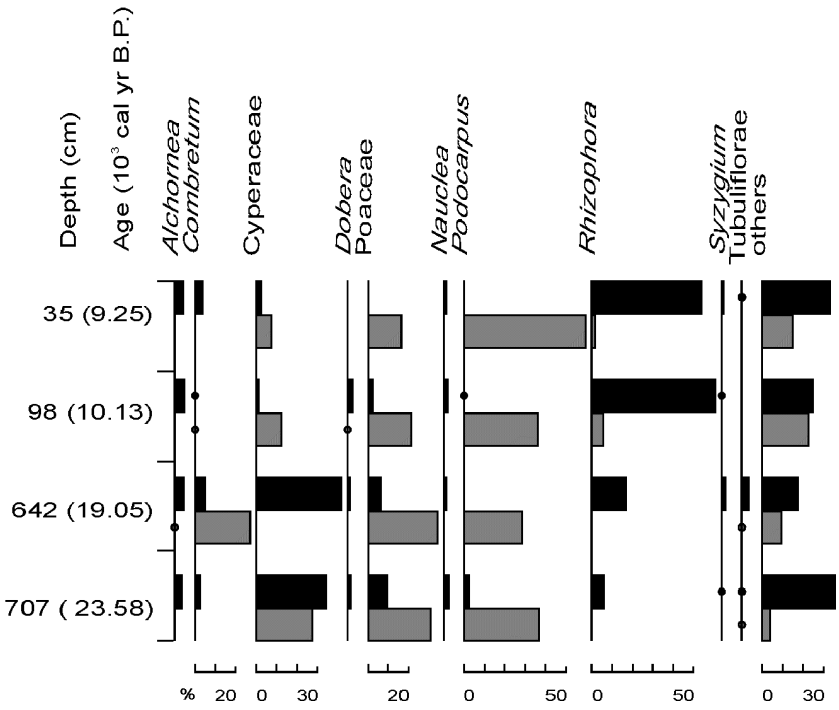

Figure 8. Percentage pollen diagram (based in pollen sum excluding spores) of selected taxa. Black bars represent fractions sieved between 5 and 10 μm and grey bars fractions sieved at 10 μm.

phora size was systematically measured (polar and equatorial axes) where possible and was found to vary between 10 and 20 μm (Fig. 9). In samples 642 cm and 707 cm, Cyperaceae dominates with subdominant *Rhizophora* and Poaceae. In all four samples, other pollen taxa of sizes between 10 and 20 μm were also identified, such as *Alchornea* and *Combretum*. Pollen grains of *Podocarpus*, exceeding 20 μm in size, were also recorded in two samples.

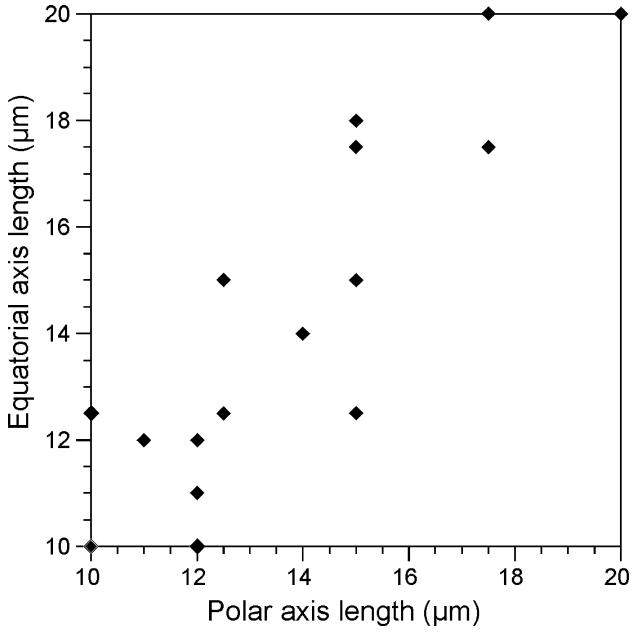

Figure 9. Polar axis length plotted against equatorial axis length of *Rhizophora* pollen grains counted in the four samples. Mean polar axis length = 14.68 μm, σ = 2.2 μm; mean equatorial axis length = 15.30 μm, σ = 2.76 μm (44 pollen grains measured).

B.2. Fraction >10 μm

On the whole, the occurrence of *Rhizophora* is low, and absent in samples 642 cm and 707 cm. In addition to the high occurrence of *Podocarpus*, Cyperaceae, and Poaceae are highly abundant, especially in the lower part of the core.

These data indicate that *Rhizophora* pollen grains are common in the fraction below 10 μm, even though they are greater than 10 μm in size. In addition, other floristic elements such as Cyperaceae or Poaceae, which are reliable indicators of open vegetation on the adjacent continent, are also found in abundance in the fraction below 10 μm. Components of the lowland rainforest or the savannah have also been identified in this fraction. It appears that monofilament mesh stretches in use so the apertures can exceed those stated; this explains the passage of pollen grains larger than the mesh aperture used. Sieving at 10 μm using monofilament mesh has often been used in palynological preparation of marine core sediments from west Africa (e.g., Dupont and Weinelt, 1996; Dupont et al., 2000; Fredoux and Tastet, 1993; Jahns, 1996; Marret, 1994) and it may therefore be assumed that the signal of sea-level rise or highstands

recorded by the occurrence of *Rhizophora* could have been missed or misinterpreted in these studies.

References

Armentrout, J.M., Fearn, L.B., Rodgers, K., Root, S., Lyle, W.D., Herrick, D.C., Bloch, R.B., Snedden, J.W., Nwankwo, B., 1999. High-resolution sequence biostratigraphy of a lowstand prograding deltaic wedge: Oso Field (late Miocene), Nigeria. In: Jones, R.W., Simmons, M.D. (Eds.), Biostratigraphy in Production and Development Geology, Special Publication-Geological Society of London, vol. 152, pp. 259–290.

Barusseau, J.P., Giresse, P., Faure, H., Lezine, A.M., Masse, J.P., 1988. Marine sedimentary environments on some parts of the tropical and equatorial margins of Africa during the late quaternary. Continental Shelf Research 8, 1–21.

Dupont, L.M., Agwu, C.O.C., 1991. Environmental control of pollen grain distribution patterns in the Gulf of Guinea and offshore NW-Africa. Geologische Rundschau 80, 567–589.

Dupont, L.M., Weinelt, M., 1996. Vegetation history of the savanna corridor between the Guinean and the Congolian rainforest during the past 150,000 years. Vegetation History and Archaeobotany 5, 273–292.

Dupont, L.M., Wyputta, U., 2003. Reconstructing pathways of aeolian pollen transport to the marine sediments along the coastline of SW Africa. Quaternary Science Reviews 22, 157–174.

Dupont, L.M., Jahns, S., Marret, F., 2000. Vegetation change in equatorial West Africa: time-slices for the last 150 ka. Palaeogeography, Palaeoclimatology, Palaeoecology 155, 95–122.

Dupont, L.M., Donner, B., Schneider, R., Wefer, G., 2001. Mid-pleistocene environmental change in tropical Africa began as early at 1.05 Ma. Geology 29, 195–198.

Ellison, J.C., 1989. Pollen analysis of mangrove sediments as a sea-level indicator: assessment from Tongatapu, Tonga. Palaeogeography, Palaeoclimatology, Palaeoecology 74, 327–342.

Fairbanks, R.G., 1989. A 17,000 year glacio-eustatic sea level record: Influence of glacial melting rates on the younger dryas event and deep-sea circulation. Nature 342, 637–642.

Fredoux, A., 1994. Pollen analysis of deep-sea core in the Gulf of Guinea-vegetation and climatic changes during the last 225,000 years BP. Palaeogeography, Palaeoclimatology, Palaeoecology 109, 317–330.

Fredoux, A., Tastet, J.-P., 1993. Analyse pollinique d'une carotte marine au large de la Côte d'Ivoire. Variations de la végétation et du climat depuis 225 000 ans BP. Palynosciences 2, 173–188.

Germeraad, J.H., Hopping, C.A., Muller, J., 1968. Palynology of tertiary sediments from tropical areas. Review of Palaeobotany and Palynology 6, 189–348.

Giresse, P., 1980. Carte sédimentologique du plateau continental du Congo. Notice explicative, editions ORSTOM Paris 85, 1–24.

Giresse, P., Bongo-Passi, G., Delibrias, G., Duplessy, J.C., 1982. La lithostratigraphie des sédiments hémipélagiques du delta profond du fleuve Congo et ses indications sur les paléoclimats de la fin du Quaternaire. Bulletin Société Géologique de France 7, 803–815.

Grindrod, J., Moss, P., van der Kaars, S., 1999. Late quaternary cycles of mangrove development and decline on the north Australian continental shelf. Journal of Quaternary Science 14, 465–470.

Grindrod, J., Moss, P., van der Kaars, S., 2002. Late quaternary mangrove pollen record from continental shelf and ocean cores in the north Australian-Indonesian region. In: Kershaw, P., David, B., Tapper, N., Penny, D., Brown, J. (Eds.), Bridging Wallace's Line: The Environmental and Cultural History and Dynamics of the SE-Asian-Australian Region. Advances in Geoecology 34 pp. 119–146.

Hoorn, C., 1994. Fluvial palaeoenvironments in the intracratonic Amazonas Basin (early Miocene-early middle Miocene Columbia). Palaeogeography, Palaeoclimatology, Palaeoecology 109, 1–54.

Jahns, S., 1996. Vegetation history and climate changes in West Equatorial Africa during the late pleistocene and holocene, based on a marine pollen diagram from the Congo fan. Vegetation History and Archaeobotany 5, 207–213.

Jansen, J.H.F., Dupont, L.M., 2001. Data report: a revised composite depth record for site 1077 based on magnetic susceptibility and XRF core scanner (CORTEX) data. Proceedings Ocean Drilling Program. Scientific Results 175, 1–10.

Koch, B.P., Harder, J., Lara, R.J., Kattner, G., 2005. Selective microbial degradation of mangrove derived isoprenoid alcohols in surface sediments. Organic Geochemistry 36, 237–285.

Lambeck, K., 1986. Glaciation and sea-level change for Ireland and the Irish Sea since late Devensian/Midlandian time. Journal of the Geological Society 153, 853–872.

Lézine, A-M., 1997. Evolution of the West African mangrove during the late quaternary: a review. Géographie Physique et Quaternaire 51, 405–414.

Lézine, A.-M., Vergnaud-Grazzini, C., 1993. Evidence of forest extension in west Africa since 22,000 BP: a pollen record from the eastern tropical Atlantic. Quaternary Science Reviews 12, 203–210.

Marret, F. 1994. Evolution paléoclimatique et paléohydrologique de l'Atlantique est-équatorial et du proche continent au Quaternaire terminal. Contribution palynologique (kystes de dinoflagellés, pollen et spores). PhD thesis, University of Bordeaux I. 271 pp.

Marret, F., Scourse, J.D., Jansen, J.H.F., Schneider, R., 1999. Changements climatiques et paleoceanographiques en Afrique Central Atlantique au cours de la derniere deglaciation: Contribution palynologique. Comptes Rendus. Académie des Sciences (Paris) 329, 721–726.

Marret, F., Scourse, J.D., Versteegh, G., Jansen, J.H.F., Schneider, R., 2001. Integrated marine and terrestrial evidence for abrupt Congo River palaeodischarge fluctuations during the last deglaciation. Journal of Quaternary Science 16, 761–766.

Morley, R.J., 1995. Biostratigraphic characterization of system tracts in Tertiary sedimentary basins. Proceedings of International Symposium on Sequence Stratigraphy, SE Asia, pp. 49–71.

Morley, R.J., Richards, K., 1993. Gramineae cuticle: a key indicator of late cenozoic climatic change in the Niger Delta. Review of Palaeobotany and Palynology 77, 119–127.

Peltier, W.R., 1994. Ice age paleotopography. Science 265, 195–201.

Pickett, J.W., Macphail, M.K., Partridge, A.D., Pole, M.S., 1997. Middle miocene palaeotopography at Little Bay, near Maroubra, New South Wales. Australian Journal of Earth Sciences 44, 509–518.

Poumot, C., 1989. Palynological evidence for eustatic events in the tropical Neogene. Bulletin des Centres de Récherches Exploration-Production Elf-Aquitaine 13, 437–453.

Richards, P.W., 1996. The Tropical Rain Forest, An Ecological Study, Second ed. Cambridge Univ. Press, Cambridge.

Shackleton, N.J., Berger, A., Peltier, W.R., 1991. An alternative astronomical calibration of the lower pleistocene timescale based on ODP Site 677. Transactions of the Royal Society of Edinburgh: Earth Sciences 81, 251–261.

Shi, N., Dupont, L.M., 1997. Vegetation and climatic history of southwest Africa: a marine palynological record of the last 300,000 years. Vegetation History and Archaeobotany 6, 117–131.

Stuiver, M., Reimer, P.J., Bard, E., Beck, J.W., Burr, G.S., Hughen, K.A., Kromer, B., McCormac, F.G., van der Plicht, J., Spurk, M., 1998. INTCAL98 radiocarbon age calibration, 24,000-0 cal BP. Radiocarbon 40, 1041–1084.

van Campo, E., 1986. Monsoon fluctuations in two 20,000-Yr BP oxygen-isotope/pollen records off southwest India. Quaternary Research 26, 376–388.

van Campo, E., Bengo, M.D., 2004. Mangrove palynology in recent sediments off Cameroon. Marine Geology 208, 315–330.

van der Kaars, S., Wang, X., Kershaw, P., Setiabudi, D.A., 2000. A late quaternary palaeoecological record from the Banda Sea, Indonesia: Patterns of vegetation, climate and biomass burning in Indonesia and Northern Australia. Palaeogeography, Palaeoclimatology, Palaeoecology 155, 135–153.

van der Zwan, C.J., Brugman, W.A., 1999. Biosignals from the EA field, Nigeria. In: Jones, R.W., Simmons, M.D. (Eds.), Biostratigraphy in Production and Development Geology. Special Publication-Geological Society of London 152, pp. 291–301.

Versteegh, G., Schefuβ, E., Dupont, L., Marret, F., Sinninghe Damsté, J.S., Jansen, J.H.F., 2004. Taraxerol and rhizophora pollen as proxies for tracking past mangrove ecosystems. Geochimica and Cosmochimica Acta 68, 411–422.

White, F., 1983. The Vegetation of Africa. UNESCO, Paris.